Using radio-tracking and direct observation to estimate roe deer *Capreolus capreolus* density in a fragmented landscape: a pilot study

A.J. Mark Hewison, Jean-Marc Angibault, Bruno Cargnelutti, Aurélie Coulon, Jean-Luc Rames, Emmannuel Serrano, Hélène Verheyden & Nicolas Morellet

Hewison, A.J.M., Angibault, J.M., Cargnelutti, B., Coulon, A., Rames, J.L., Serrano, E., Verheyden, H. & Morellet, N. 2007: Using radio-tracking and direct observation to estimate roe deer *Capreolus capreolus* density in a fragmented landscape: a pilot study. - Wildl. Biol. 13: 313-320.

In this pilot study, we estimate roe deer *Capreolus capreolus* density in a fragmented landscape, using radio-tracking and direct observation in a Petersen-Lincoln framework with the joint hypergeometric maximum likelihood estimator. We used radio-tracking to obtain a direct count of the number of marked animals potentially observable in a given sample area, thus avoiding edge effects. We then carried out a coordinated observation survey, including drive beating, to ascertain the proportion of marked roe deer in the population sampled and thus generate a population estimate. Surveys were repeated three times in four sample blocks within the fragmented landscape, and estimates were compared to a sample block of a central forest in the same area. In general, roe deer are difficult to observe and census, but our experimental set-up in the fragmented landscape enabled us to observe on average 75% of marked animals present in a given survey (compared to 21.5% in the central forest). The variability in capture probability between individuals was low as three quarters of all marked individuals were observed in all, or all but one, of the surveys. Density estimates were largely similar across the sample blocks of the fragmented landscape (4.0-7.9 deer/100 ha), but lower than in the central forest (34.3 deer/100 ha). The variability of daily population estimates was quite low and similar in the fragmented landscape (CV of 25.9%) and the central forest (CV of 25.3%). Taking availability of woodland into account, the density in the fragmented landscape was as high, or higher, than in the central forest, reaching an exceptional 145.3 deer/100 ha of woodland in one survey area.

Key words: Capreolus capreolus, capture-mark-recapture, density, edge effects, roe deer, ungulates, woodland fragmentation

A.J. Mark Hewison, Jean-Marc Angibault, Bruno Cargnelutti, Aurélie Coulon, Jean-Luc Rames, Emmannuel Serrano, Hélène Verheyden & Nicolas Morellet, Comportement et Ecologie de la Faune Sauvage, Institut National de la Recherche Agronomique, BP 52627, CASTANET-TOLOSAN Cedex, F 31326 FRANCE - e-mail addresses: Mark.Hewison@toulouse.inra.fr (A.J. Mark Hewison); jmangib@toulouse.inra.fr (Jean-Marc Angibault); bcargnel@toulouse.inra.fr (Bruno Cargnelutti); ac462@cornell.edu (Aurélie Coulon); Jean-Luc.Rames@toulouse.inra.fr (Jean-Luc Rames); emmanu@ozu.es (Emmannuel Serrano); Helene.Verheyden@toulouse.inra.fr (Hélène Verheyden); Nicolas.Morellet@toulouse.inra.fr (Nicolas Morellet)

Corresponding author: A.J.M. Hewison

Received 2 June 2005, accepted 28 June 2006

Associate Editor: John D.C. Linnell

Estimating animal abundance is a major obstacle for wildlife researchers and managers alike (Seber 1982, Williams et al. 2002). This is particularly the case for woodland species such as the roe deer *Capreolus capreolus* which is secretive and hence difficult to observe (see Gaillard et al. 1993) compared to other ungulate species living in more open habitats (e.g. bighorn *Ovis canadensis*: Bodie et al. 1995; elk *Cervus elaphus*: Cogan & Diefenbach 1998; and caribou *Rangifer tarandus*: Mahoney et al. 1998). The roe deer has undergone a recent demographic expansion at the European scale (Danilkin & Hewison 1996, Andersen et al. 1998) and has concomitantly colonised new and more open habitats (Hewison et al. 1998). At present, the species is found in landscapes with varying degrees of forest fragmentation where distribution and ranging behaviour depend on landscape structure (Lovari & San José 1997, Hewison et al. 2001, Cargnelutti et al. 2002, Coulon et al. 2004).

The problem of estimating roe deer abundance was first highlighted by Andersen (1953), who described an experiment in which the population number was first estimated using traditional methods applied by hunters in the course of their yearly census for management purposes. Subsequently, the whole population was shot in order to assess the accuracy of the hunters' estimate. The final count was more than three times higher than the original estimate of 70 deer. Since then, some authors have suggested alternative methods to estimate roe deer density, including using distance sampling, e.g. line transects (Gaillard et al. 1993), strip transects (Zejda 1984), pellet group counts (McIntosh et al. 1995), vocalisations (Reby et al. 1998) or indices of abundance to provide temporal trends (e.g. the kilometric index; Vincent et al. 1991). Techniques based on capture-mark-recapture (Pollock et al. 1990) remain the most reliable tools to provide estimates of population density of roe deer in closed habitats (e.g. Gaillard et al. 1986). However, as yet there is no information available in the literature on estimating population density of roe deer in a fragmented landscape context.

In this paper, we describe a pilot study to estimate roe deer population density in a fragmented landscape within a Petersen-Lincoln framework (see also Strandgaard 1967, McCullough & Hirth 1988), using the joint hypergeometric maximum likelihood estimator (White 1996, White & Shenk 2001). More precisely, our method comprises the use of radio-tracking to determine the exact number of marked animals present during each survey of sample plots (see Eberhardt 1990), thus avoiding edge effects (*sensu* Seber 1986), followed by recapture through direct observation. Further, we report average and between-individual heterogeneity in the probability of observing a roe deer in such a landscape. We also compare density estimates and parameter values with those derived from a similar approach carried out in a non-fragmented forest within the same area.

Material and methods

Study site

Our study was carried out in a fragmented landscape in the canton of Aurignac (N 43°13', E 0°52'), situated in the Comminges region of southwestern France along the Nère valley. It is a hilly region, rising to a maximum of 380 m a.s.l., which has undergone substantial modification due to intensification of agricultural practice leading to a loss of hedges and copse, planting of new crop types (corn *Zea mays*, sorghum *Sorghum* spp.) and an increase in average field size. This has resulted in a mixed landscape of open fields and small woodland patches (average size of 3 ha), with a central larger forest of 800 ha. The primary land use is pastoral for sheep and cattle grazing, but with agricultural crops increasing. The total study area covers about 7,500 ha of which about 25% are wooded (Fig. 1). The human population is present throughout the site, in small villages and farms distributed along the extensive road network which covers the study site.

The natural vegetation of the area is classified as a southwest European lowland-colline downy oak forest (Bohn et al. 2004). At present, the landscape is characterised by woodland patches dominated by oak *Quercus* spp., often associated with hornbeam *Carpinus betulus*, whereas the central forest is a mixed species forest of Douglas-fir *Pseudotsuga menziesii*, pine *Pinus* spp., oak and hornbeam. The understorey is dominated by brambles *Rubus* spp.,

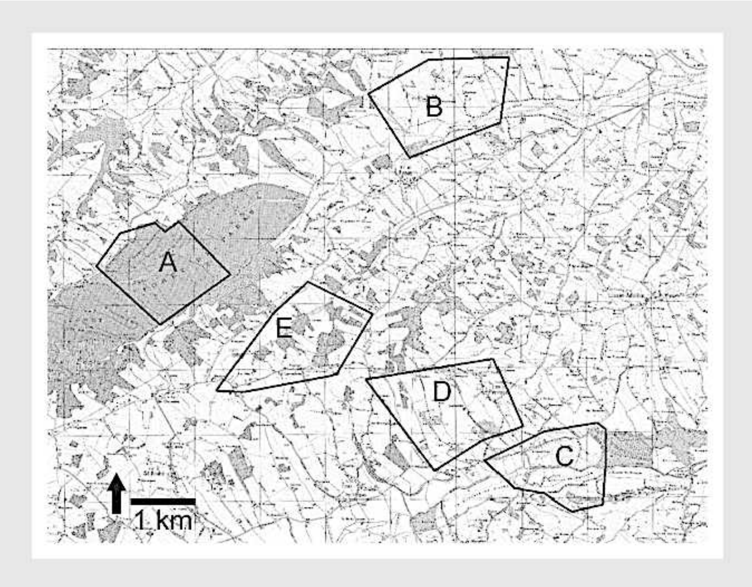

Figure 1. Study area showing the four sample blocks in the fragmented landscape (B-E) and the central forest block (A). Wooded habitat is indicated in grey.

common honeysuckle *Lonicera peryclimenum*, ivy *Hedera helix* and butcher's broom *Ruscus aculeatus*. The climate is oceanic with an average annual temperature of 11-12 °C and 800 mm of precipitation, mainly in the form of rain.

In the forest, the visibility is limited to around 35 m on average, but ranges within < 5 - > 100 m depending on understorey structure. In the fragmented zones roe deer may be observed up to 800 m away, but are more generally seen at a distance of < 400 m.

The roe deer population is hunted on a regular basis by drive hunts with dogs during winter (September-January) and stalking during summer (June-August; bucks only). The hunting teams are organised at the communal level such that each sample block (see below) is hunted by a different team. Roe deer density in the central forest was previously estimated at around 20 deer/100 ha (Reby et al. 1998). No density estimates are available for the surrounding fragmented landscape, but standardised car transects during winter (counts of all roe deer seen along a 85-km circuit of the study site, repeated at dawn and dusk 6-10 times per year during February-March) indicate a relatively stable population during 1992-2001, followed by a decrease in 2002 and a subsequent increase.

Study population

We caught roe deer during winter using large-scale drives of 30-100 beaters and up to 4 km of long-nets. Deer were weighed, sexed, equipped with radio-collars (either Biotrack or Televilt VHF systems, or Lotek GPS systems) and released on site. The collars were individually identifiable by the colour code of rubber strips attached to the collar. In the winter of 2004/05, we caught 19 roe deer in the central forest and 23 deer in the surrounding fragmented landscape. The majority of marked roe deer in the fragmented landscape were concentrated in four separate zones (Table 1), hence for this study we carried out data collection in these four zones plus the central forest area.

Data collection

For each zone, we considered the area that was beaten during the roe deer catch as the sample block. Hence, we defined five blocks, one in the central forest and four in the surrounding fragmented landscape (see Fig. 1), covering 123-301 ha (see Table 1). The block boundaries were generally roads or tracks and were often situated on hill crests, affording good visual cover of the sample block (except for the central forest). Up to 19 marked roe deer were potentially present in the central forest sample block, and 5-7 in each of the fragmented landscape sample blocks. We carried out data collection between 10 March and 8 April 2005. After the catching operations were completed and once the hunting season had closed, data collection was carried out during 2-3 hour surveys which took place just after sunrise or just before sunset, when roe deer are most active (Jeppesen 1989).

Table 1. Characteristics and parameters obtained during the three observation surveys for estimating roe deer population density in four sample blocks (B-E in Fig. 1) of a fragmented landscape. M gives the number of marked animals present, and m the number of marked animals observed out of the total number of observed animals (n) for a given survey. See text for details about the calculation methods.

Sample block	Surface area (ha)	Woodland (ha)	Survey	M	m	n	Petersen-Lincoln population estimate	m/M (%)
Fabas plain (B)	301	15	1	6	5	20	23.5	83.3
			2	4	4	16	16.0	100
			3	6	5	22	25.8	83.3
Embargade (C)	123	19	1	5	4	8	9.8	80.0
			2	3	3	6	6.0	100
			3	4	2	7	12.3	50.0
Touch mort (E)	221	55	1	5	4	17	20.6	80.0
			2	4	4	15	15.0	100
			3	4	1	6	16.5	25.0
Peyrissas (D)	275	21	1	3	1	4	9.0	33.3
			2	4	3	12	15.3	75.0
			3	5	5	10	10.0	100

Immediately prior (< 1 hour) to each survey in a given sample block, we first radio-tracked all collared animals in the area using a RX 100 Televilt receiver and a Yagi antennae in order to establish the number of marked individuals that were present within the boundaries of the block to be surveyed, and hence potentially observable. The location of these marked animals was also verified at the end of the survey. Subsequently, a team of four observers conducted the survey in the following manner: for sample blocks located in the fragmented landscape, two observers used a series of vantage points along the block boundaries to survey the area. Simultaneously, the remaining two observers walked along parallel pre-determined transects, cutting through the block and visiting all woodland patches and other closed habitats. The four observers progressed through the sample block in a synchronised manner and maintained constant radio contact using hand-held radios. All observations of roe deer during the survey were noted, along with the time and the location. Roe deer were identified to sex, age class (juvenile or adult) and whether they were radio-collared or not (otherwise, as 'unidentified'). When marked, the observer identified the individual roe deer by the colour code of the collar using binoculars and/or a telescope. In some cases, a few animals with radio collars which no longer worked were present in the survey blocks. As the presence of these animals in a given block could not be determined *a priori* by radio-tracking methods, for the purposes of the surveys, when observed, these animals were considered as unmarked. To avoid any double-counting, observers notified their colleagues of deer observations in real time by radio. In the central forest, we followed the same procedure with the following exception: because visibility was much poorer (see above), all observers moved along pre-determined transects within the sample block. The transects were sufficiently distant so as to ensure that roe deer were unlikely to be counted twice (see Reby et al. 1998).

Statistical analysis

We considered the four sample blocks situated in the fragmented landscape as four spatially independent surveys for estimating deer density in this fragmented landscape (blocks separated by on average 2.6 km, but see below). We compared parameter estimates and variability of these four blocks with those for the central forest. For each of the four blocks in the fragmented landscape, we carried out three survey repetitions on different days (with at least two days between surveys of a given block) and for the central forest block we carried out eight survey repetitions. We considered the separate surveys as replicates for a given block.

For each replicate, following Eberhardt (1990), we calculated a Petersen-Lincoln estimate of population size using Chapman's (1951) modification of the standard Petersen-Lincoln equation:

$$\hat{N} = \frac{(M_i + 1)(n_i + 1)}{(m_i + 1)} - 1$$

where M_i is the number of marked animals in the study block during the ith survey, n_i = the number of animals observed during the ith survey, and m_i is the number of marked animals in the observed sample. In our study, M_i was the number of radio-collared animals in the study block at the time of each survey.

Following Eberhardt (1990), from the individual replicate estimates, we calculated a coefficient of variation for each sample block derived from the usual sample estimate of the variance as:

$$S^2 = \frac{\sum(\hat{N}_i - \bar{\hat{N}})^2}{k - 1}$$

where k is the number of daily surveys conducted.

We then calculated average population size for a given sample block using the joint hypergeometric maximum likelihood estimator proposed by White (1996) in the NOREMARK software. Because the survey blocks were not geographically closed, we used the Immigration-Emigration extension of this estimator (Neal et al. 1993, White 1996), which allows for animals moving on and off the study area through a binomial process where a known number of marked animals M_i of the possible T_i animals with transmitters is present in the block for the ith survey (White 1996). We assumed that the blocks were demographically closed, as no hunting occurred during the survey period, and natural mortality is likely insignificant over the short period considered.

Results

In the fragmented landscape, we observed a variable, but on average high (> 75%), proportion of the marked deer present in a given study block (see Table 1). Indeed, on four of 12 survey occasions, we observed all of the marked roe deer in a particular block. This compared to a much lower average value of 21.5% of marked roe deer observed in the central forest block during the eight surveys (Table 2).

Density estimates in three of the four sample blocks in the fragmented landscape were not significantly different, with average estimates of 7.2 (CI : 6.6-9.2), 7.3 (CI : 6.5-10.6) and 7.9 (CI : 6.6-11.1) roe deer per 100 ha. In the fourth sample block (Peyrissas), density was significantly lower (non-overlapping confidence intervals) at 4.0 (CI: 3.5-6.3) roe deer per 100 ha. Density was estimated as 4-8 times higher in the central forest block (see Table 2). When taking into account the different availability of woodland habitat in the different sample blocks, the density estimate for the central forest block (100% woodland; density of 34.3 deer/100 ha) was quite similar to that in three of the four blocks (24.7, 15.4 and 7.5% woodland; density of 31.6, 46.8 and 52.4 deer/100 ha of woodland, respectively) in the fragmented landscape. When taking into account woodland availability, density in the most open site (Fabas plain) was considerably higher (5.0% woodland; density of 145.3 deer/100 ha woodland). Var-

Table 2. Characteristics and parameters obtained during eight observation surveys for estimating roe deer population density in the central forest sample block (A in Fig. 1) of 159 ha (100% woodland). M gives the number of marked animals present, and m the number of marked animals observed out of the total number of observed animals (n) for a given survey. See text for details about the calculation methods.

Survey	M	m	n	Petersen-Lincoln population estimate	m/M (%)
1	18	8	17	37.0	44.4
2	17	2	7	47.0	11.8
3	17	2	5	35.0	11.8
4	18	5	19	62.3	27.7
5	16	4	17	60.2	25.0
6	15	1	5	47.0	6.7
7	15	5	16	44.3	33.3
8	18	2	9	62.0	11.1

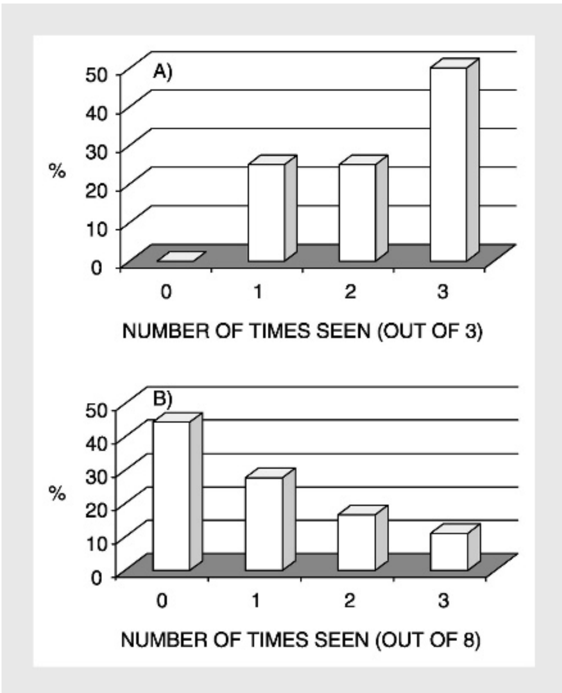

Figure 2. Proportion of individual roe deer that were seen 0-3 times during the three surveys in each sample block of the fragmented landscape (A) and the eight surveys in the central forest sample block (B).

iability of density estimates across surveys for a given sample block was generally not high, and was similar in the fragmented landscape (average CV = 25.9%; range: 16.7-34.0%) and in the central forest block (average CV = 25.3%; range: 15.3-29.5%, for three surveys sampled randomly from the pool of eight, repeated four times).

Among the marked roe deer, we observed low heterogeneity in observation probabilities of individuals in the fragmented landscape. Of the marked animals which were present in the sample block on each of the three survey occasions, 75% were observed at least twice and none of them were never observed (Fig. 2A). By comparison, of the marked animals present on at least three sample occasions in the central forest sample block, almost half (44%) were never seen and only 28% were observed on two or more occasions (out of eight surveys; Fig. 2B). No marked animal was observed more than three times out of eight in the central forest block.

Discussion

Using radio-tracking and direct observation surveys, we were able to generate quite precise estimates of roe deer population density in a fragmented landscape. While surveys were carried out in rather small sample blocks relative to roe deer home-range size, using radio-tracking prior to and following each survey allowed us to directly assess the number of marked individuals present, and hence potentially observable, in the surveyed block. Using this approach, we were able to avoid edge effects, that is, partial exposure to capture for animals with ranges that are only partly included within the surveyed area (Eberhardt 1990, Neal et al. 1993, White & Shenk 2001). While the number of marked animals per study block was relatively small (5-7), significant bias in density estimates is unlikely as we consistently observed a high proportion of marked animals (see below), although it may lead to wider confidence intervals. Our study highlighted some noteworthy points which are worth further discussion.

First, during the surveys we observed a high proportion of the marked animals present in the fragmented sample blocks, notably in comparison to the central forest block. In fact, in the fragmented landscape most of the animals were seen most of the time; at least three quarters of marked animals were observed in 75% of the surveys (see Table 1). In contrast, in the central forest $<$ 30% of marked animals were observed in 75% of the surveys (see Table 2). Furthermore, although we were unable to test this formally due to the small sample size (only 12 deer were present on all three survey occasions in the fragmented landscape blocks), the assumption of equal probability of re-capture (observation) between individuals was most likely respected; most marked roe deer (75%) were observed either twice or three times (out of three surveys) and no marked roe deer were never observed (see Fig. 2A).

These observation probabilities are extremely high for this rather shy and secretive species which is generally difficult to observe. Clearly, the observability of roe deer, and undoubtedly other ungulates, is landscape specific. Indeed, it seems that roe deer have a low tolerance of disturbance and hence a long flight distance in these relatively open landscapes. As a result, the two central observers often acted as beaters in that they provoked early flight, allowing the other observers to successfully identify the individual roe deer. By maintaining constant radio contact during the observation surveys, we were able to effectively eliminate problems arising from double counting in almost all cases. The only possibility of counting the same individual animal twice occurred when unmarked deer took flight in the direction of the survey transect, so that it may have settled further along and may have been re-observed at a later time during the same survey. This was rarely a problem as when flight of deer was provoked, they tended to escape outside the sample block or circle behind the advancing observer line (see Reby et al. 1998). However, we did sometimes re-observe marked animals a second time during the course of a single survey (eight times in the fragmented blocks and only once in the central forest block), indicating that we also likely observed some unmarked animals more than once in a given survey. Such undetected re-observation of unmarked animals, if frequent, may lead to inflated estimates of population size.

The estimates of roe deer density that we generated for the fragmented landscape were remarkably similar for three of the four sample blocks, but somewhat lower for the fourth (around half the density value). These blocks cannot be considered as true replicates within the fragmented landscape as habitat factors and variable hunting pressure may lead to spatial variation in local density levels. However, it seems likely that the spatial proximity of some of the blocks (see Fig. 1) and the somewhat larger roe deer home-range sizes in fragmented landscapes (Cargnelutti et al. 2002) mean that there is some degree of dependence, as deer may move from one block to another in the course of normal ranging activity (A.J.M. Hewison, B. Cargnelutti, J.M. Angibault & N. Morellet, unpubl. data).

While the average deer density was estimated to be lower in the fragmented landscape (4.0-7.9 roe deer/100 ha) than in the central forest (34.3 roe deer/100 ha), this does not take into account differences in landscape structure. Despite recent range expansion, roe deer are traditionally considered to be a woodland species (Hewison et al. 1998), preferentially exploiting the forest edge (Hansson 1994, Tufto et al. 1996), and have some degree of spatial attachment to woodland habitat in almost all landscapes (Lovari & San José 1997, Hewison et al. 2001). When considering the availability of woodland habitat, density in the fragmented landscape was as high or higher than that of the central forest which itself carried what can be considered as a high density roe deer population (*cf*. Vincent et al. 1995). Indeed, in the most open sample block, deer density per 100 ha of woodland was 145.3, which is exceptionally high for this species. However, in such a landscape, with around only 5% of woodland, roe deer are expected to extensively exploit the habitat matrix and may spend a large proportion of their time in fields, hedgerows and meadows (Aulak & Babinska-Werka 1990, Cibien et al. 1995). This seems to be supported by our radio-tracking data (A.J.M. Hewison, B. Cargnelutti, J.M. Angibault & N. Morellet, unpubl. data) and suggests that roe deer adapt their foraging and ranging behaviour to the landscape context in a highly plastic manner.

Our study presents an effective method for obtaining density estimates of roe deer in a fragmented landscape, which are likely accurate in view of the high proportion of animals observed during surveys. This might suggest that direct censussing of roe deer is possible in certain landscape contexts for management purposes. However, this is not our intention; rather, we suggest that the method presented here will be more appropriately employed in a research context. Instead, we believe that managers would do better to employ an approach based on indicators, as estimates of density *per se* may not be that useful for large scale management objectives (see Cederlund et al. 1998). Indeed, indices of abundance (Caughley 1977) and other indicators of ecological change are often easier to measure and may be more appropriate for managing wildlife populations (Morellet et al. 2007).

Acknowledgements - we thank J.P. Chanal and the local hunting associations for allowing us to work in the central forest block and the surrounding fragmented area, respectively, and M. Sarasa for help in the field. We thank two anonymous referees for comments on an earlier version of this paper. During this study, A. Coulon was supported by a grant from the Fédération Départementale des Chasseurs de la Haute Garonne and the Fédération Régionale des Chasseurs de Midi-Pyrénées, and E. Serrano by a postdoctoral grant from INRA, France.

References

Andersen, J. 1953: Analysis of a Danish roe-deer population (Capreolus capreolus (L)) based upon the extermination of the total stock. - Danish Review of Game Biology 2: 127-155.

Andersen, R., Duncan, P. & Linnell, J.D.C. 1998: The European roe deer: the biology of success. - Scandinavian University Press, Oslo, 376 pp.

Aulak, W. & Babinska-Werka, J. 1990: Use of agricultural habitats by roe deer inhabiting a small forest area. - Acta Theriologica 35: 121-127.

Bodie, W.L., Garton, E.O., Taylor, E.R. & McCoy, M. 1995: A sightability model for bighorn sheep in canyon habitats. - Journal of Wildlife Management 59: 832-840.

Bohn, U., Gullub, G., Hettwer, C., Neuhäuslova, Z., Schlüter, H. & Weber, H. 2004: Map of the natural vegetation of Europe. Scale 1:2.500.000. - Interactive CD-ROM (S. Hennekens), Bonn-Bad Godesberg. Federal Agency for Nature Conservation: Map of the natural vegetation of Europe. Scale 1:2.500.000. - Federal Agency for Nature Conservation.

Cargnelutti, B., Reby, D., Desneux, L., Angibault, J.M., Joachim, J. & Hewison, A.J.M. 2002: Space use by roe deer in a fragmented landscape - some preliminary results. - Revue d'Ecologie (Terre Vie) 57: 29-37.

Caughley, G.J. 1977: Analysis of vertebrate populations. - John Wiley & Sons, New York, USA, 234 pp.

Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R.B., Gaillard, J.M., Boisaubert, B., Ballon, P. & Duncan, P. 1998: Managing roe deer and their impact on the environment: maximising the net benefits to society. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); The European roe deer: the biology of success. Scandinavian University, Oslo, pp. 337-372.

Chapman, D.G. 1951: Some properties of the hypergeometric distribution with applications to zoological sample censuses. - University of California Publications in Statistics 1: 131-160.

Cibien, C., Bideau, E., Boisaubert, B., Biran, H. & Angibault, J.M. 1995: Seasonal diet and habitat use in field roe deer (Capreolus capreolus) in the Picardie region. - Gibier Faune Sauvage 12: 37-49.

Cogan, R.D. & Diefenbach, D.R. 1998: Effect of undercounting and model selection on a sightability-adjustment estimator for elk. - Journal of Wildlife Management 62: 269-279.

Coulon, A., Cosson, J.F., Angibault, J.M., Cargnelutti, B., Galan, M., Morellet, N., Petit, E., Aulagnier, S. & Hewison, A.J.M. 2004: Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. - Molecular Ecology 13: 2841-2850.

Danilkin, A. & Hewison, A.J.M. 1996: Behavioural ecology of Siberian and European roe deer. - Chapman and Hall, London, 275 pp.

Eberhardt, L.L. 1990: Using radio telemetry for mark-recapture studies with edge effects. - Journal of Applied Ecology 27: 259-271.

Gaillard, J-M., Boisaubert, B., Boutin, J.M. & Clobert, J. 1986: L'estimation d'effectifs à partir de capture-marquage-recapture: application au chevreuil (Capreolus capreolus). - Gibier Faune Sauvage 3: 143-158. (In French).

Gaillard, J-M., Boutin, J.M. & Van Laere, G. 1993: Dénombrer les populations de chevreuils par l'utilisation du line transect. Etude de faisabilit. - Revue d'Ecologie (Terre Vie) 48: 73-85. (In French).

Hansson, L. 1994: Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. - Landscape Ecology 9: 105-115.

Hewison, A.J.M., Vincent, J.P., Joachim, J., Angibault, J.M., Cargnelutti, B. & Cibien, C. 2001: The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. - Canadian Journal of Zoology 79: 679-689.

Hewison, A.J.M., Vincent, J.P. & Reby, D. 1998: Social organisation of European roe deer. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); The European roe deer: the biology of success. Scandinavian University, Oslo, pp. 189-219.

Jeppesen, J.L. 1989: Activity patterns of free-ranging roe deer (Capreolus capreolus) at Kalø. - Danish Review of Game Biology 13: 1-30.

Lovari, S. & San José, C. 1997: Wood dispersion affects home range size of female roe deer. - Behavioural Processes 40: 239-241.

Mahoney, S.P., Virgl, J.A., Fong, D.W., MacCharles, A.M. & McGrath, M. 1998: Evaluation of a mark-resighting technique for woodland caribou in Newfoundland. - Journal of Wildlife Management 62: 1227-1235.

McCullough, D.R. & Hirth, D.H. 1988: Evaluation of the Petersen-Lincoln estimator for a white-tailed deer population. - Journal of Wildlife Management 52: 534-544.

McIntosh, R., Burlton, F.W.E. & McReddie, G. 1995: Monitoring the density of a roe deer Capreolus capreolus population subjected to heavy hunting pressure. - Forest Ecology and Management 79: 99-106.

Morellet, N., Gaillard, J-M., Hewison, A.J.M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F. & Maillard, D. 2007: Indicators of ecological change: new tools for managing populations of large herbivores. - Journal of Applied Ecology 44: 634-643.

Neal, A.K., White, G.C., Gill, R.B., Reed, D.F. & Olterman, J.H. 1993: Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. - Journal of Wildlife Management 57: 436-450.

Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. 1990: Statistical inference for capture-recapture experiments. - Wildlife Monographs 107: 1-97.

Reby, D., Hewison, A.J.M., Cargnelutti, B., Angibault, J.M. & Vincent, J.P. 1998: Use of vocalizations to estimate population size of roe deer. - Journal of Wildlife Management 62: 1342-1348.

Seber, G.A.F. 1982: The estimation of animal abundance and related parameters. 2nd edition. - Macmillan, New York, USA, 654 pp.

Seber, G.A.F. 1986: A review of estimating animal abundance. - Biometrics 42: 267-292.

Strandgaard, H. 1967: Reliability of the Petersen method tested on a roe deer population. - Journal of Wildlife Management 31: 643-651.

Tufto, J., Andersen, R. & Linnell, J. 1996: Habitat use and ecological correlates of home range size in a small cervid: the roe deer. - Journal of Animal Ecology 65: 715-724.

Vincent, J.P., Bideau, E., Hewison, A.J.M. & Angibault, J.M. 1995: The influence of increasing density on body weight, kid production, home range size and winter grouping in roe deer. - Journal of Zoology 236: 371-382.

Vincent, J.P., Gaillard, J-M. & Bideau, E. 1991: Kilometric index as a biological indicator for monitoring forest roe deer populations. - Acta Theriologica 36: 315-328.

White, G.C. 1996: NOREMARK: Population estimation from mark-resighting surveys. - Wildlife Society Bulletin 24: 50-52.

White, G.C. & Shenk, T.M. 2001: Population estimation with radio-marked animals. - In: Millspaugh, J.J. & Marzluff, J.M. (Eds.); Radio tracking and animal populations. Academic Press, San Diego, USA, pp. 329-350.

Williams, B.K., Nichols, J.D. & Conroy, M.J. 2002: Analysis and management of animal populations. - Academic Press, San Diego, 817 pp.

Zejda, J. 1984: Road strip transects for estimating field roe deer density. - Folia Zoologica 33: 109-124.